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Art. II.—*On Coprosma Baueri, Endlicher.*

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(With Plate IV.)

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1. The Genus.

Coprosma is a genus of Rubiaceæ, comprising some 60 species, whose headquarters are in New Zealand. The Dominion and its dependencies possess 39 of these species(1), Australia five(2), and the remaining units extend northward to New Guinea and Borneo, and westward to the Sandwich Islands and Juan Fernandez, near the Pacific coast of South America. The New Zealand species form dense thickets, both in lowland forests and in woods to heights of 6000 feet. They vary very much in mode of growth and foliage at different periods of their life history. Many Coprosmas have the aspect of desert plants, as have also New Zealand species of *Pennantia*, *Hoheria* and *Plagianthus*, and are consequently termed xerophytes. These show great range of variability in their leaves; the seedling and mature stages possessing larger leaves than the intermediate one. This xerophytic habit, so strongly represented in the flora of a temperate, well watered group of islands, has been a fertile source of discussion by biologists and geologists. Hutton(3) asserts that during the Pliocene period the Southern Alps were much higher than now, and that such groups as the Chatham and Auckland Islands were part of the New Zealand mainland. The plains east of the main ridge were arid and wind-swept, with warm summers, and very cold winters. Dr. L. Cockayne(4) explains that the seedling stage of these plants of xerophytic aspect, and with an alternation of leaf forms, represents the ancestral plant before the Pliocene desiccation; the intermediate foliage represents the plant of Pliocene New Zealand; and the larger leaves of the mature form are the response to present conditions. Two erect species with large coriaceous shining leaves are commonly cultivated in public and private gardens throughout Australia—*C. Baueri*, Endl., and *C. lucida*, Forst.

2. Previous workers.

Cheeseman(5), in an article on "New Zealand Species of Coprosma," refers to the curious little pits that exist on the under surface of the leaves of these plants, states that they are often inhabited by a tiny yellow acarid, but confesses that he is unable to guess as to their function.

Dr. A. N. Lundström (6) applied to the pits the name domatia, and decided that they were of use to the plant as the home of commensals, living in symbiosis with it. Mr. Alexander Hamilton(7)

1 The numbers refer to works consulted, shown in the Bibliography at the end of the paper

gave a general review of these curious leaf organs, dealing especially with the histology of the leaf of *Pennantia Cunninghamii*, Miers, and figuring a hair from the pit of *Coprosma lucida*, Forst. Both of these writers(6, 7) lay much stress on the use of the pits as a habitation for Acarina, though Hamilton acknowledges that as often as not the pits were found without guests. Where mites were numerous he found the walls of the cavities damaged, showing brownish patches and bright crimson cells. It is remarkable that the kaikomako or New Zealand Pennantia is in its young state a shrub, whose flexuous interlacing branches and small distant sessile leaves give it the aspect of a xerophyte; while in its mature stage it is a tree, 20 to 30 feet high, with stalked glossy leaves two inches in length. A very important paper on the Coprosma leaf pits is that by Miss N. A. R. Greensill(8), dealing with the minute structure of the leaves of ten New Zealand species, and reviewing all work on the subject to date. Miss Greensill utterly failed to find insect guests in the so-called *domatia*, either in species cultivated in gardens and public parks, or in those growing under natural conditions; she found some pits in an unhealthy state with brown patches and crimson-coloured cells, but traced these changes to attacks of fungi. Miss Greensill favours the view that the pits absorb moisture. Mr. Nathan Banks(9) figures three structures in leaves caused by Acarina, which he terms dimple gall, capsule gall, and pouch gall respectively, caused by mites *Eriophyes pyri*. The pear-leaf blister mite is found in Australia.

3. Histology.

I. Leaf Structure of C. Baueri.

The pits lie on each side of the midvein, at junctions with primary veins, and vary in number from four to nine; those in the lower part of the leaf are often immature and closed, when the upper ones are mature and open. Very rarely are they found on the primary veins; and in each case noted this abnormal position was limited to a single pit. In transverse section, (fig. 1), the leaf shows an upper epidermis of three layers. The first is constructed of small ovate cells, with their longitudinal axis parallel to the surface, irregular in size, the longest about 31 μ. This layer is clothed externally by cutin measuring one-half to one-third the transverse diameter of a cell. The units of the second layer show no cell contents, and are polygonal in outline; their greatest diameter is 65 μ. The third layer is composed of cells (fig. 2) showing transition forms between those of the second layer and palisade cells, the shape is rhomboidal or rhombo-polygonal, and the long axis is at right angles to the surface, the greatest length is 33 μ. Palisade cells proper are in three rows, slender in outline, 54 long, three or four abutting on each pair of third rank epidermal cells. The spongy parenchyma (fig. 1), shows cells of various outlines—oval, globular, dumb-bell shaped, etc., seldom exceeding 35 μ in diameter. The intercellular spaces between them are very small; with the exception of those near a pit they communicate by numerous small stomata.

with the outer air. Stomata are of usual type, surrounded by the ordinary epidermal cells, which have not the wavy outline common to their class. The lower epidermis is of a single layer of minute rounded-oval cells, raised into short bluntly conical points on their free surfaces (fig. 3). Numerous unicellular hairs coat this lower leaf surface, most of which spring from an inflated base (fig. 3), and sometimes from a pear-shaped cell, larger than the epidermal cells among which it is inserted.

II. The Leaf Pits. (Fig. 1).

In transverse section the pits present various irregular shapes, and widen rapidly from their openings. In common with other portions of the lower epidermis, these pits are beset with numerous unicellular nucleated and non-nucleated hairs. Each pit is lined with epidermal cells, clothed outwardly with cutin, and set with the longitudinal axis at right angles to the surface. Though the spaces in the spongy parenchyma may only be separated from the outer air by two layers of cells, no stomata have been found in these depressions.

III. The Veins. (Fig. 1.)

In transverse section the midrib presents an upper epidermis of a single layer of cells, resembling those of the outer layer in the blade. Beneath this is a mass of cortical cells, most thickly developed on the lower surface, and enclosing a vascular bundle, of which the xylem elements form the upper, and the phloem elements the lower, portion of the bundle, as is usual in dicotyledonous leaves. A well marked pericycle surrounds the whole, its cells blending into the mass of cortical cells on the upper margin. In smaller veins the bundle sheath is formed of large cells, whose outer walls are considerably thickened, and when the vein is cut at right angles the sheath resembles a minute necklace. The vessels of the xylem are mainly spirally strengthened, and those of the protoxylem are exceedingly slender and delicate.

IV. The Stem. (Figs. 5 and 6.)

In transverse section, fig. 5, the stem is peculiar for the depth of the bast layer, and for the way in which it gradually merges into the phelloderm of the cortex. The only difference in transverse section between phloem and phelloderm is the direction of the longitudinal axis in their cells, in the former running radially, in the latter circumferentially. The phellogen shows clearly, and there is a layer of empty cells below the dead cork.

In longitudinal section, (fig. 6), the elements of bast and wood are particularly interesting, especially in reference to the xylem and phloem parenchyma, which are very well represented. The wood parenchyma is exactly of the type illustrated by Strasburger (11), as are also the tracheides, with narrow oblique bordered pits, figured by that author under the term *fibre tracheides*. In tangential section the medullary rays

are three to four cells thick, the elements unequal in size, and arranged in oblique series. The cells are evidently of two types, the outer ones showing circular bordered pits, which in the inner cells are absent.

4. The Functions of the Pits.

My colleague, C.A.L., examined a large number of leaves in Melbourne gardens, and in no case found insect guests inhabiting the pits; an examination of plants in the Sydney Botanic Gardens in January, 1921, and in the Brisbane Botanic Gardens in October, 1921, also gave negative results. Miss Greensill reports similarly of her experience of New Zealand species of Coprosma. This seems to dispose of Lundström's theory that the pits are the homes of commensals. To test whether these pores are sources of a supply of moisture to the leaf, similar to those figured by Kerner and Oliver(12) the pits on healthy leaves, still attached to the plant, were filled by C.A.L. with a quickly drying varnish, and flourished as well as ever, proving that absorption through the pores is no necessary function. It has already been stated that the pits do not contain stomata, and that these organs are minute in size, and numerously spread over the surface of the lower epidermis. After exhausting the aids of the microscope and of experiment, our conclusion is that the pores were formerly of assistance to the plant when under xerophytic conditions, and that in the Miocene age of continental New Zealand, the stomata were confined to them, as in the leaves of many of our Hakeas, but that with modern and more humid conditions, the leaves have developed stomata on their lower epidermis, and the pits are now useless to the plant, having only an interest to the teleologist.

EXPLANATION OF PLATE IV.

Fig. 1—Transverse section of leaf.
- e. Pit.
- f. Midrib.

Fig. 2—a. Epidermis and cutin.
- b. Epidermal cells of second layer.
- c. Palisade cells.

Fig. 3—Epidermis, underside of leaf.

Fig. 4—Upper epidermis, surface.

Fig. 5—Transverse section of young twig.

Fig. 6—Tangential section.
- a. Medullary rays.
- b. Fibre tracheids.
- c. Trachea.

Fig. 7—Basal membrane of pit.

Fig. 8—Nucleated hair from base of pit.

BIBLIOGRAPHY.

1. Cheeseman, T. F.—Manual of the New Zealand Flora, 1906, p. 243.
2. Bentham—Flora Australiensis, Vol. III., pp. 429–30.

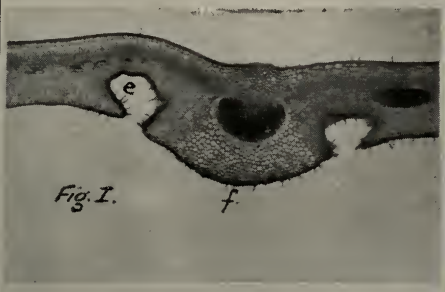

Fig. I.

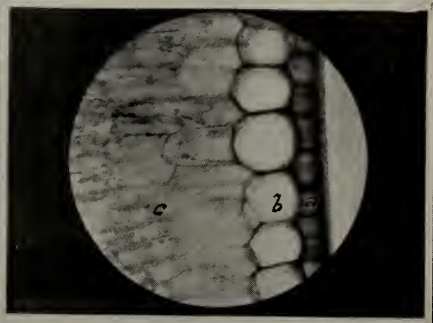

FIG. 2

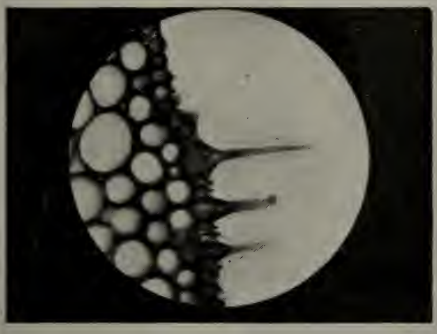

FIG. 3

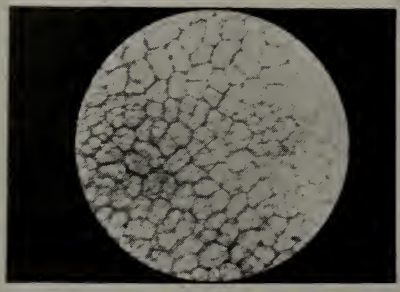

FIG. 4

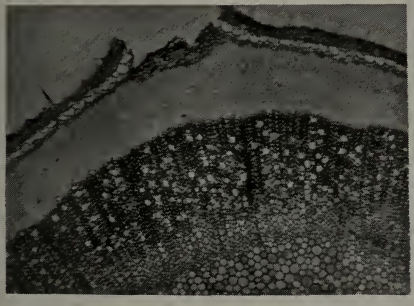

FIG. 5

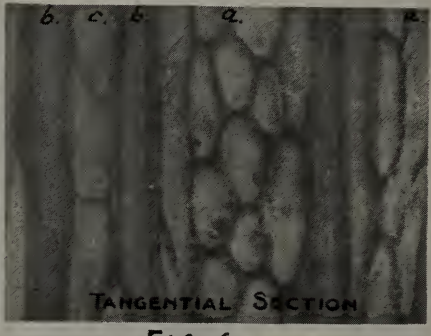

FIG. 6

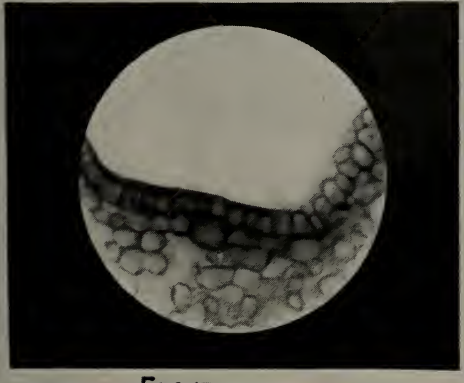

FIG.7

FIG. 8